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Climate change impacts on vernal pool hydrology and vegetation in northern California

Ashton Montrone[a,1], Laurel Saito[b,*,2], Peter J. Weisberg[c], Meredith Gosejohan[c,3], Kyle Merriam[d], John F. Mejia[e]

[a] Graduate Program of Hydrologic Sciences, University of Nevada Reno, 1664 N. Virginia Street, Mail Stop 0175, Reno, NV 89557, USA
[b] Department of Natural Resources and Environmental Science and Graduate Program of Hydrologic Sciences, University of Nevada Reno, 1664 N. Virginia Street, Mail Stop 0186, Reno, NV 89557, USA
[c] Department of Natural Resources and Environmental Science, University of Nevada Reno, Mail Stop 0186, Reno, NV 89557, USA
[d] Sierra Cascade Province, USDA Forest Service, 159 Lawrence St., Quincy, CA 95971, USA
[e] Division of Atmospheric Sciences, Desert Research Institute, 2215 Raggio Parkway, Reno, NV, 89512, USA

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ABSTRACT

Vernal pools are seasonal wetlands that have a high diversity of endemic and native plant species, yet they are threatened by agricultural conversion and urban development and face threats posed by climate change resulting from altered precipitation and temperature regimes. We developed an approach to investigate the potential impacts of climate change on hydrology and vegetation communities of vernal pools by creating a mass-balance hydrologic model that is coupled to a statistical model of plant community distribution. The hydrologic and vegetative models were calibrated using field measurements from a vernal pool in northeastern California that experiences snow-dominated hydrology and is larger than vernal pools in more studied areas like Central California, but representative of other northern California vernal pools. Using downscaled data from global climate models, the coupled model suggests that warmer conditions will lead to the pool being inundated for a shorter time, but with little change in maximum depth. Reduced hydroperiods suggest possible declines in vernal pool specialist species with future climate change. The coupled model is an integrated approach for understanding the impact of altered environmental conditions on unique hydrology and plant community composition of vernal pool ecosystems, but the model approach could be improved with longer term data and by applying it at more sites to broaden the applicability of the approach and to enable better process representation.

1. Introduction

Vernal pools are ephemeral wetlands that exist in local topographic depressions with relatively impermeable substrates (Keeley and Zedler, 1998; Boone et al., 2006). In temperate regions experiencing winter snowfall like northern California, they are subject to four distinct seasons: they typically 1) fill with snow in the winter, 2) melt into inundated pools in the spring, 3) become unsaturated and vegetated by summer, and then 4) dry and become fully desiccated by autumn. Their main source of water is direct precipitation, though some pools receive runoff from a very small watershed (Keeley and Zedler, 1998). The substrates of vernal pools can be bedrock such as volcanic mud or lava flows, clay rich soils, cemented mudflow, and soils with hard clay pans or duripans (Hobson and Dahlgren, 1998; Keeley and Zedler, 1998; Smith and Verrill, 1998; Boone et al., 2006). All of these substrates have low hydraulic conductivities. As these low permeability substrates restrict the infiltration of water, small amounts of precipitation can produce perched zones of saturation and pooling of water (Rains et al., 2008).

The ephemeral nature of vernal pools and associated vegetation is also influenced by climate. Vernal pools are distinguished by the source and seasonality of their water inputs. Vernal pools associated with Mediterranean climates can receive a majority of precipitation in the cooler months of the winter, whereas summers are hot and dry (Keeley and Zedler, 1998). Vernal pool vegetation distribution varies from year to year depending on climatic conditions such as precipitation amount

* Corresponding author at: The Nature Conservancy, 1 E. First Street, Suite 1007, Reno, NV 89501, USA.
E-mail addresses: laurel.saito@tnc.org (L. Saito), pweisberg@cabnr.unr.edu (P.J. Weisberg), kmerriam@fs.fed.us (K. Merriam), john.mejia@dri.edu (J.F. Mejia).
[1] Present address: Hydrometrics, Inc., 3020 Bozeman, Helena, MT 59601, USA.
[2] Present address: The Nature Conservancy, 1 E. First Street, Suite 1007, Reno, NV 89501, USA.
[3] Present address: Susanville Indian Rancheria, 745 Joaquin Street, Susanville, CA 96130, USA.

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Table 1
Summary of previous modeling studies of vernal pools, including this study.

Study	Location	Model description	Key findings
Pyke (2004)	Santa Barbara County and Oroville, CA, USA	PHYDO water balance model; modeled 45 vernal pools; each pool modeled as rectangular prism; also modeled water temperature	• Model represented daily depths most closely when volume declined, but deviated more during early season filling • Geomorphology limited pool volume for Oroville pools in Central Valley, whereas amount of precipitation limited pool volume for coastal pools in Santa Barbara • Magnitude and timing of precipitation were primary controls on vernal pool hydrology • One set of pools were monitored 3–4 days a week, and the other set were observed every two weeks, contributing to model uncertainty
Pyke (2005)	Central Valley, CA	PHYDO water balance model (see Pyke, 2004); modeled 4 sites along a latitudinal gradient	• Climate change scenarios indicated hydroperiod increased with higher temperature and precipitation • Evaluation of projected changes on seven branchiopods indicated increased surpluses of inundation days needed for reproduction
Boone et al. (2006)	Cloquet, MN, USA	Water balance model; modeled eight vernal pools separately; each pool modeled as cylinder of constant area	• Modeled pool depths were reasonable for the first two years, but were not as well represented in third year • Infiltration rates specific to each vernal pool are necessary • Measured depths are needed to parameterize models • Unaccounted-for groundwater flow could have affected results
Maclean et al. (2012)	Lizard Peninsula, Cornwall, UK	Used approach of Pyke (2004) with water volume and up to 4 soil layers; modeled 18 basins that included permanent and ephemeral water bodies; used Lidar-based area/volume regression for water bodies	• Modeled water depths had Nash-Sutcliffe efficiencies varying between 0.225 and 0.946 for the 18 basins • Accounting for interbasin water exchanges is important for simulations • Run-time was a limitation when accounting for interbasin exchanges • Hydroperiod was sensitive to basin land use, basin shape, curve numbers, and basin slope steepness
This study	Northeastern CA, USA	Water balance model; modeled one vernal pool; pool volume/area curve constructed from survey data; model linked to habitat for plant communities	• Simulated pool hydrology represented measured hydrology well • Climate change reduced hydroperiod • Vernal pool specialists likely to decline with climate change

and timing as well as air temperature (Brooks, 2004; Keeley and Zedler, 1998). Because vernal pools have seasonally distinct climatic conditions (i.e., alternating between inundation and desiccation for months at a time), unique plant communities are found within the pools. Plant communities in vernal pools transition from one to another along subtle topographic gradients based on hydrologic thresholds (Keeley and Zedler, 1998; Gosejohan et al., 2017). Vernal pool plant species must cope with inundated conditions during the time of seed germination and seedling establishment, and also rapid desiccation in early summer. Many species of wetland plants are not found in vernal pools because of an inability to tolerate the severe soil desiccation and heat stress that occurs during summer. Conversely, many upland grasses that can tolerate soil desiccation cannot tolerate inundation (Keeley and Zedler, 1998). Perennial grass species are found more often above the high water line, whereas vernal pool specialist species are usually found below the high water line (Bauder, 2000).

Vernal pools in northeastern California and elsewhere may be threatened by climate change (Bauder, 2005; Brooks, 2009). Dettinger and Cayan (1995) showed that air temperatures in winter months in the northern and central Sierra Nevada increased by roughly 2 °C over their period of study (1940–1995). Projections for the 21st century show temperatures increasing by 3 or 4 °C for the region under a "business as usual" scenario (Stewart et al., 2004). Precipitation did not increase in this area between 1940 and 1995 (Dettinger and Cayan, 1995) and is not projected to change through the 21st century (Stewart et al., 2004; Maurer, 2007). More recent research shows a projected increase in years with many atmospheric river precipitation events related to climate change scenarios in the northern Sierra in the 21st century, but also note that the uncertainty at regional scales is still large (Dettinger, 2011). If these temperature and precipitation projections are correct, water budgets of vernal pools in the region will likely be affected. If all other variables are held constant, a temperature increase without an increase in precipitation might lead to the pools being filled for a shorter amount of time because the increase in temperature would increase evaporation and more precipitation will fall as rain instead of snow, leading to earlier snowmelt and more rapid drying of the pool substrate (Brooks, 2009; Berghuijs et al., 2014). Vernal pool plant communities are structured primarily by hydrologic influences such as hydroperiod (inundation length) and water depth (e.g., Emery et al., 2009; Gosejohan et al., 2017), and therefore the species composition of vernal pools is expected to be sensitive to climate shifts that alter hydroperiod. Vernal pool vegetation may also be affected by changes in precipitation seasonality, given that precipitation during winter and the early growing season has been observed to favor native vernal pool specialist species, whereas late-season precipitation favors non-native plant species (Javornik and Collinge, 2016).

Because of the presence of endemic vegetation and distinct annual hydrologic patterns of vernal pools, the goals of this research were to develop a modeling approach to examine if a changing climate has the potential to shorten the period of inundation (hydroperiod) and impact vegetation patterns of the vernal pools. We coupled a hydrologic water balance model with a static model of plant community habitat associations to investigate the following hypotheses:

- Hypothesis 1: Changes to precipitation and temperature regimes associated with climate change scenarios will decrease the period of inundation in vernal pools.
- Hypothesis 2: Changes to precipitation and temperature regimes associated with climate change scenarios will decrease the maximum depth of water in vernal pools.
- Hypothesis 3: If hypotheses 1 or 2 are supported, then changes to precipitation or temperature regimes associated with climate change will result in proportionally fewer vernal pool specialist species.

Although vernal pools and their unique vegetation have been recognized for decades (Jepson, 1925; Keeley and Zedler, 1998) and there

have been several studies of their vegetation (Bliss and Zedler, 1998; Keeley, 1990; Spencer and Riesberg, 1998) as well as fauna (Baldwin et al., 2006; Simovich, 1998), few attempts to model their hydrology have been made, possibly because of the relatively small amount of water contained by vernal pools as well as their ephemeral nature. Furthermore, previous hydrologic models of vernal pools did not link model outputs to expected changes in vegetation or fauna (e.g., Pyke, 2004; Boone et al., 2006; Maclean et al., 2012; Table 1). In the current study, we linked the outputs of a hydrologic water balance model to known vernal plant community habitat associations to assess potential impacts of climate change on habitat availability for vernal pool specialist plants. While our study focuses on one vernal pool in northern California and uses data from a limited time period, our overarching objective is to demonstrate an approach that examines the hydrology and vegetation of vernal pools that can be applied in other landscapes with similar data limitations, or that can be improved where more data are available. In this article, we describe the development of the hydrology model and its linkage to a vegetation model whose development is described in detail in Gosejohan et al. (2017).

2. Site description

Our vernal pool model was developed and calibrated for Northeast Coyote Springs (hereafter referred to as Coyote Springs) in Lassen National Forest (N 40° 42′ 55″, E 121° 22′ 2″) in northeastern California (Fig. 1) as the location for this study. The elevation of Coyote Springs is 1580 mASL and the area is 4.6 ha. Unlike more frequently studied western U.S. vernal pools that are located in lower elevation valleys with mostly rain precipitation and often connected to other pools, Coyote Springs is an isolated vernal pool that receives much of its precipitation as snow. The pool is surrounded by coniferous forest composed primarily of *Calocedrus decurrens*, *Pinus ponderosa* and *Pinus jeffreyi* with an understory dominated by *Artemisia tridentata, Purshia tridentata* and several perennial grass species. Dominant plant species within the vernal pool vary by hydroperiod and water depth, with short-inundated communities of vernal pool specialist species *Epilobium brachycarpum*, *Lotus purshianus*, *Microsteris gracilis* var. *gracilis*, and *Trichostema oblongum,* and non-native *Bromus hordeaceus* and *Lactuca serriola*; moderately-inundated communities of *Deschampsia danthonioides* and *Grindelia nana*, *Cuscuta howelliana* and *Epilobium densiflorum*, and long-inundated communities of *Castilleja campestris* ssp. *campestris*, *Eleocharis bella*, *Marsilea oligospora*, *Pilularia americana*, *Plagiobothrys stipitatus*, and *Psilocarphus brevissimus* (Gosejohan, 2012; Gosejohan et al., 2017). Soils for Coyote Springs were identified as the Skalan-Bobbitt families association (Web Soil Survey, 2012) and the soils of the greater area are volcanic in origin (Norris and Webb, 1976).

The morphology of soils in volcanic northern California vernal pools can be controlled by ferrolysis, clay formation and translocation, duripan formation, and calcium carbonate formation (Rains et al., 2008). Ferrolysis occurs when soils alternate between aerobic and anaerobic conditions. When the soils are inundated with water, they become anaerobic, which creates a reducing environment where free iron is reduced to ferrous iron (Fe^{2+}) and displaces base cations. Base cations, silicates, and bicarbonate move downward in the soil profile and precipitate out of solution as the pool dries. This process forms a duripan that is thickest in the deepest parts of the pool and tapers towards the

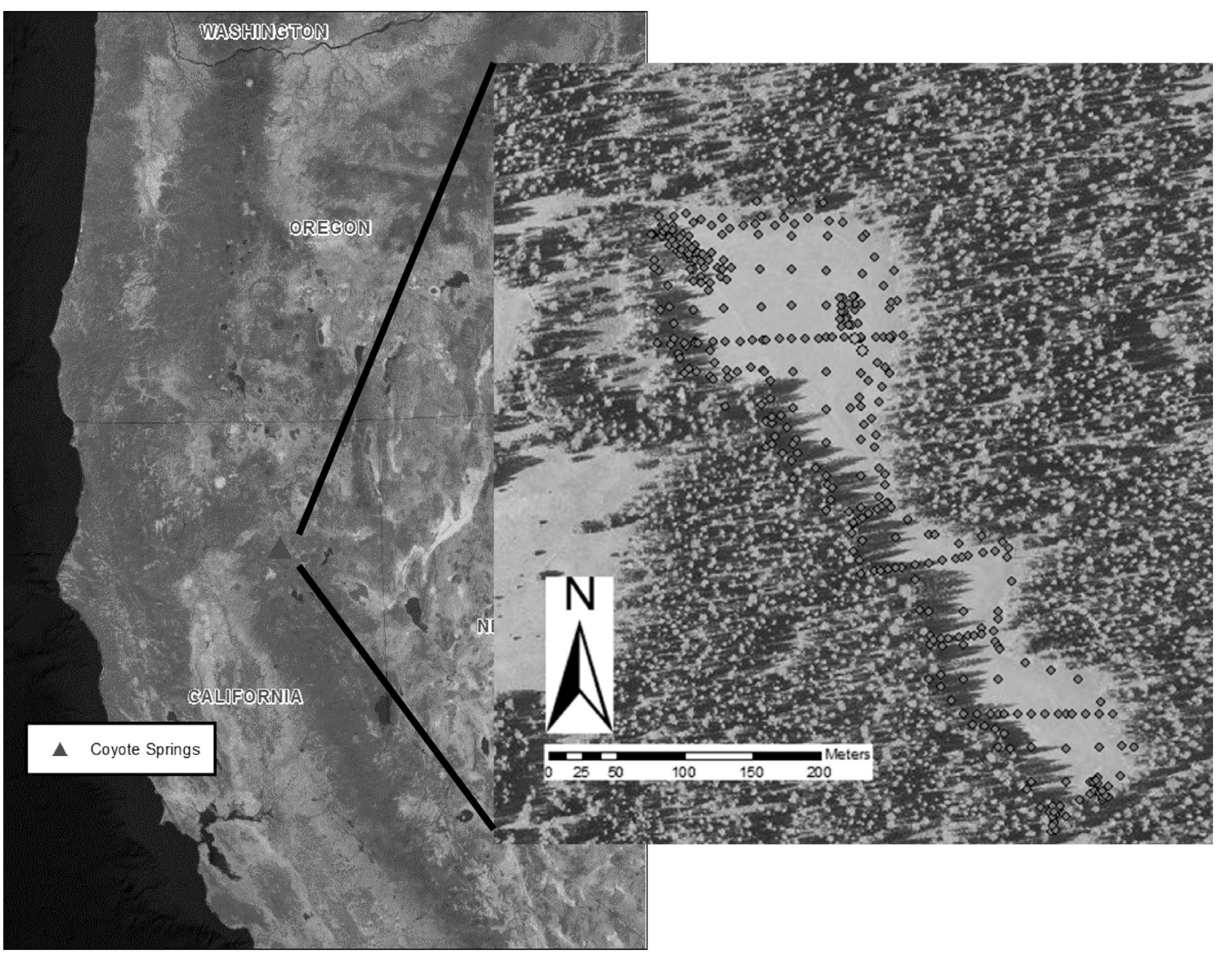

Fig. 1. General location of Coyote Springs and locations of survey points (dots) and stage gages (stars) within Coyote Springs. Many of the survey points were also vegetation survey locations. Additional survey points were recorded to capture changes in topographic features for the surface interpolation.

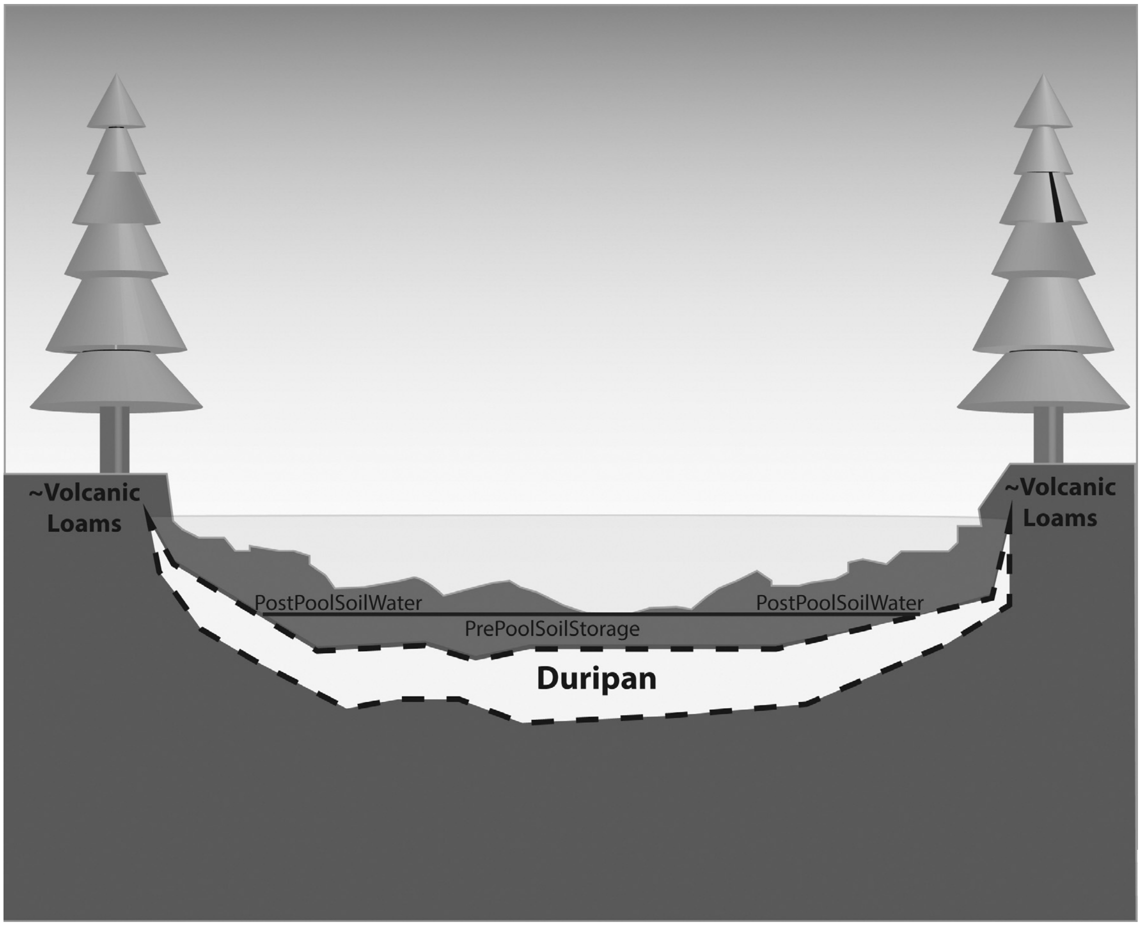

Fig. 2. Conceptual diagram of volcanic vernal pools (not to scale). The duripan is thickest at the deepest part of the pool and tapers towards the margins. As water enters the pool basin, soil pores below the black horizontal line (*PrePoolSoilStorage*) must be filled before the pool is created. When pool stage increases, water enters both the pool and soil pores above the black horizontal line. Water that enters the soil pores above the black horizontal line is *PostPoolSoilWater*.

margins of the pool basin (Hobson and Dahlgren 1998; Fig. 2). Also, the clay particles created during weathering move downward in the soil profile when the soil is saturated. As the soil profile matures, a gradient of soil texture where soil is coarser near the surface and finer soil is near the duripan develops (Hobson and Dahlgren, 1998). Soil texture analysis of Coyote Springs soils taken at the surface and at depth reflected such morphology. The aquitard of the duripan has two primary effects on the hydrology of vernal pools: 1) it inhibits percolation from the pool above into the groundwater system; and 2) it inhibits groundwater from entering the vernal pool.

3. Methods

3.1. Stage gauges and field surveys

Water depths were measured at discrete locations within the pool using mounted game cameras, and then extrapolated to the entire vernal pool at a daily time step using a detailed topographic survey (Gosejohan et al. 2017). Moultrie Game Spy I-65 digital cameras and two stage gauges were installed in December 2010 at Coyote Springs. The stage gages were placed at the deepest part of the pool; two were placed for redundancy in case one of the stage gages was damaged. The cameras were programmed to take photographs of the stage gauges every four hours throughout the day. The stage gauges were made from PVC pipe, had tape markings at 2 cm intervals, and were attached to steel rebar that was hammered into the ground. Stage measurements were recorded from the photographs from December 4, 2010 to December 12, 2011.

In summer 2011, vegetation was surveyed in 1-m^2 quadrats uniformly spaced at intersections within a 25-m grid, and also every 10-m along two fine-scale transects that ran the lengths of the major and minor axes of the pool. In each 1-m^2 quadrat, all plant species were identified and cover classes estimated using a modified Daubenmire (1959) classification. Please see Gosejohan et al. (2017) for more detail on the methods used for vegetation monitoring. A topographic survey using a Leica-Wild TC101 total station and Total Data Systems Recon with Survey Pro for Windows XP (Version 3.8.1) data collector was also performed that included the vegetation survey points, stage gauges, and topographic features such as steep elevation gradients, high points, and the pool perimeter for a total of 350 survey points over approximately 5700 m^2. The total station survey data were used to create a surface interpolation and stage:area:volume (S:A:V) relationship using kriging with 2.5-m grid resolution with Surfer Version 8.0 (Golden Software, 2002). The S:A:V relationship is a vertically discretized bathymetric surface that provides pool volume and area at a 2-cm vertical resolution. The 2-cm vertical resolution of the hydrologic and vegetation model is conservatively constrained by the coarser of these two data sets (i.e., stage gage as opposed to the total station survey). The area and volume resolution was 1-m^2 and 1-m^3, respectively.

3.2. Coupled model development

Separate hydrologic and vegetation models were developed to work together by using hydrologic model output of hydroperiod and maximum depth as input to the vegetation model. Broadly speaking, the hydrologic model was used to estimate the water depth and inundation

duration spatially across the pool, which were then used with the vegetation model to estimate vegetated community distribution.

3.2.1. Hydrologic model development

The hydrologic model was built in Excel with a time step of one quarter of a month. The length of this time step was selected as a compromise between temporally disparate datasets that ranged in frequency between daily and monthly. Monthly datasets were linearly interpolated to quarterly data sets, such as the publicly available monthly Parameter-elevation Relationships on Independent Slopes Model (PRISM; Daly et al., 1994) data, whereas daily data sets were aggregated into quarters of a month, such as the availability of vernal pool stage calibration data and water depth measurements from Gosejohan et al. (2017). On average, one quarter of a month is ≈7.6 days. Inputs to the hydrologic model were mean air temperature and precipitation over water year (WY) 2011 (see Section 3.3 for more details on the climate inputs), and the output was a time series of pool stage. Although the pool only had water for about 7 months, the model covered the entire water year to ensure that the model simulated the beginning and ending of inundation appropriately. The S:A:V relationship was used to calculate the water balance at each time step as well as the resulting pool stage at the deepest part of the pool.

As part of the water balance approach, evapotranspiration was calculated for both the soil and the open water of the pool. Potential evapotranspiration was calculated using the Hamon (1963) simplification of the Thornthwaite method (Hamon, 1963; Thornthwaite, 1948). Potential evapotranspiration (PET in mm) was converted to actual evapotranspiration using coefficients unique to the soil and open water (Eqs. (1) and (2)). The coefficients α_{Water} and α_{Soil} were obtained through the calibration process described in Section 3.2.2. Although this approach does not directly account for water stress, which can be important under arid conditions, we applied this simplified approach because of limited data availability in future climate simulations.

$$AET_{Soil} = 1000 * \alpha_{Soil} PET \tag{1}$$

AET_{Soil} = actual soil evapotranspiration [m]
α_{Soil} = soil actual evapotranspiration coefficient [unitless]

$$AET_{Water} = 1000 * \alpha_{Water} PET \tag{2}$$

AET_{Water} = actual water evapotranspiration [m]
α_{Water} = water actual evapotranspiration coefficient [unitless]

The S:A:V relationship was used to calculate the evapotranspiration volume from AET_{Water} that was then multiplied by the area of the pool from the previous time step (Eq. (3)).

$$WVE = AET_{Water} * (PoolArea_{t-1}) \tag{3}$$

WVE = water volume evapotranspiration [m^3]
Pool Area$_{t-1}$ = pool area from S:A:V used in the previous time step [m^2]

To calculate the evapotranspiration from the soil, AET_{Soil} was multiplied by the maximum pool area minus the pool area from the previous time step (Eq. (4)).

$$SVE = AET_{Soil} * (Maxpool - [PoolArea_{t-1}]) \tag{4}$$

SVE = soil volume evapotranspiration [m^3]
MaxPool = maximum possible pool area [m^2]

The maximum pool area was defined by the area of a polygon drawn around the interface of the surrounding trees and pool basin because the area adjacent to the pool is not much higher topographically and therefore contributes little water to the pool via runoff. *MaxPool* was determined to be 46,000 m^2.

Precipitation volume input for each timestep was calculated by multiplying the precipitation for a quarter month by the maximum pool area (Eq. (5)).

$$PrecipVolume = Precip * MaxPool \tag{5}$$

PrecipVolume = water volume of precipitation [m^3]
Precip = precipitation rate for a quarter of a month [m/quarter of a month]

The phase of the precipitation (i.e., rain or snow) was determined using the Water and Snow Balance Modeling System (WASMOD) method (Xu, 2002). In the WASMOD method, the phase of precipitation is a function of mean air temperature (Eqs. (6) and (7); mean air temperature was calculated as the average of minimum temperature and maximum temperature for each timestep).

$$sn_t = p_t \left\{1 - e^{[(c_t - a_1)/(a_1 - a_2)]^2}\right\} \tag{6}$$

sn_t = solid part of snow [m^3]
p_t = precipitation [m^3]
c_t = mean air temperature [°C]
a_1 = air temperature above which all precipitation is rain [°C]
a_2 = air temperature above which snow melting begins [°C]

$$r_t = p_t - sn_t \tag{7}$$

r_t = rainfall [m^3]

a_1 and a_2 were calibration parameters for the model. Rainfall enters directly into the soil and pool. Snow is added to the snowpack (Eq. (8)) and must melt before it is added to the soil and pool. The melting function is also defined by the WASMOD approach as a function of the a_1 and a_2 parameters (Eq. (9)).

$$sp_t = sp_{t-1} + sn_t - m_t \tag{8}$$

sp_t = snowpack [m^3]
m_t = snowmelt [m^3]
sp_{t-1} = snowpack from previous time step [m^3]

$$m_t = sp_{t-1} \left\{1 - e^{-[(c_t - a_2)/(a_1 - a_2)]^2}\right\} \tag{9}$$

Water could leave the system by seepage through the duripan (Eq. (10)). The seepage rate was defined as a function of stage (Eq. (11)).

$$Seepage = PoolArea_{t-1} * SeepageRate \tag{10}$$

Seepage = seepage volume [m^3]
SeepageRate = rate of seepage [m/quarter of a month; Eq. (11)]

$$SeepageRate = SeepageCoeff^{(c)PoolStage_{t-1}} \tag{11}$$

SeepageCoeff = calibration parameter [m/quarter of a month]
c = conversion factor with a value of 1 [m^{-1}]
PoolStage$_{t-1}$ = pool stage from previous time step [m]

The model was constructed such that when pool stage increased, the volume of water associated with the stage increase conceptually entered two places: the open-water pool and the unwetted soil pores above the previous depth (Fig. 2). The flux of water associated with water entering the unwetted soil pores was called the *PostPoolSoilWater* (Eq. (12)). Partitioning of water between the pool and *PostPoolSoilWater* was determined by the *BasinSoilFactor* and was calibrated to be a value between 0 and 1. The remaining fraction of precipitation entered the pool.

$$PostPoolSoilWater = precipitation * BasinSoilFactor \tag{12}$$

PostPoolSoilWater = volume of water diverted to soil when stage increases [m^3]
BasinSoilFactor = calibrated factor that partitions precipitation between soil and pool when stage is increasing [unitless]

Before the pool could be created, the soil pore volume between the lowest elevation in the pool basin (see the horizontal black line in Fig. 2) and the duripan (*PrePoolSoilStorage*) was required to be filled with water. *PrePoolSoilStorage* could range from zero to $PrePoolSoilStorage_{Max}$ (Eq. (13)).

$$PrePoolSoilStorage_{Max} = MaxPool * SoilDepth * Porosity \tag{13}$$

$PrePoolSoilStorage_{Max}$ = maximum volume of storage in *PrePoolSoilStorage* [m^3]
SoilDepth = calibrated average depth of soil between lowest elevation and duripan [m]
Porosity = fraction of soil volume occupied by pores [unitless]

The *SoilDepth* used to calculate *PrePoolSoilStorage* was a calibration parameter. *MaxPool* and *Porosity* were user-specified values. While a full texture analysis was not possible at Coyote Springs, Iubelt et al. (2016) found surface soils in four nearby pools with similar morphology to have sandy loam, loam, and clay loam texture. *Porosity* was set to 0.5, which is consistent with silt loam (0.485), clay loam (0.476), and silty clay (0.492) (Clapp and Hornberger, 1978). As soil properties could not be measured, using *SoilDepth* as a calibration parameter helped to approximate the volume of *PrePoolSoilStorage* as a function of *Porosity* and *SoilDepth*. Water was not routed into the pool until *PrePoolSoilStorage* reached $PrePoolSoilStorage_{Max}$.

Another water storage in the model was snowpack (Eq. (8)). Precipitation that fell as snow was added to the snowpack. Water in the snowpack did not enter the *PrePoolSoilStorage* or pool until it melted. The model assumed the water did not re-freeze.

A third water storage was the open-water pool (referred to as "the pool"). Water was allowed to exchange between the *PrePoolSoilStorage* and the pool.

After the model calculated the balance of the fluxes from the system of equations for a timestep, the balance was added (positive or negative) to the *PrePoolSoilStorage* (Eq. (14)):

$$PrePoolSoilStorage = m + r - Seepage - WVE - SVE \tag{14}$$

The model then evaluated if the *PrePoolSoilStorage* was at maximum capacity. If the *PrePoolSoilStorage* was above maximum capacity, excess water was routed to the pool. Otherwise, the model routed water from the pool back to *PrePoolSoilStorage* until $PrePoolSoilStorage_{Max}$ was reached, or left *PrePoolSoilStorage* below $PrePoolSoilStorage_{Max}$ if there was no water in the pool (Fig. 3).

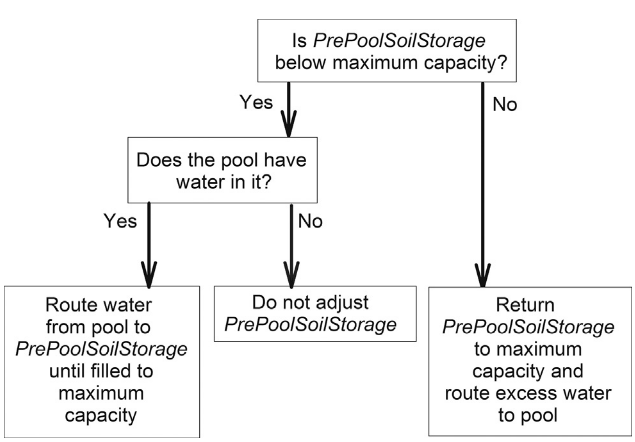

Fig. 3. Decision tree that determined water routing in and out of the pool.

3.2.2. Hydrologic model calibration

The calibration metrics used for fitting the model parameters were root-mean-squared error (RMSE) for water depth over 33 temporal observations and hydroperiod difference at the stage gages (Eq. (15)). The RMSE was only calculated over the period when there was water in the pool to be more conservative in calculating the RMSE.

$$Hydroperiod\ Diff = \frac{|Obs.\ Hydroperiod - Modeled\ Hydroperiod|}{Obs.\ Hydroperiod} \tag{15}$$

HydroperiodDiff = hydroperiod difference [no. of timesteps]
Obs. Hydroperiod = hydroperiod observed from stage gauges [no. of timesteps]
Mod. Hydroperiod = modeled hydroperiod [no. of timesteps]

HydroperiodDiff was a calibration metric to penalize differences between modeled and observed pool hydroperiods where each timestep was one quarter of a month. Early calibration efforts using RMSE alone resulted in parameter values that wetted the pool later and dried the pool earlier than was observed. This disproportionately affected the deepest parts of the pool. As vernal pool specialist species are typically found in the deeper parts of the pool (Bauder, 2000), it was important that the parameter values selected model the period of inundation well for this portion of the pool. *InitialSoilStorage* is a parameter that is defined as the volume of water that is in the soil at the start of the model and is calibrated for (Table 2).

A Monte Carlo approach was used because there can be multiple optimal parameter sets for this model. Random non-integer values were selected from a uniform distribution of the specified range of values for each parameter and solver function in Excel was executed to minimize the sum of RMSE and *HydroperiodLengthDiff* by adjusting parameter values. This procedure was executed 200 times. The final calibrated parameter values were the values for the model run that had the smallest sum of RMSE and *HydroperiodLengthDiff* of the 200 Monte Carlo runs (Table 2).

3.2.3. Vegetation model development

The vegetation model was developed as a statistical model that relates the probability of occurrence for a given plant community type to the inundation length (hydroperiod) and maximum depth associated with a 1-m^2 frame within which vegetation was sampled (see Section 3.1 for details). The model was developed by coupling data gathered from the vegetation survey with stage gage data as described in Gosejohan et al. (2017). The overall approach was similar to that of Auble et al. (1994), where riparian plant community types were positioned along a gradient of inundation duration using a direct gradient approach, allowing projections of how changes in river management would alter plant community composition. Gosejohan et al. (2017) used non-metric multidimensional scaling (NMS) ordination analysis to determine that inundation length and maximum depth were predictive hydrologic variables for vernal pool plant species. Hierarchical agglomerative cluster and indicator species analyses (Dufrêne and Legendre, 1997) were used to group the sites according to plant species composition, into five broad plant community types defined by annual hydroperiod and maximum water depth: short-term inundated, edge, shallow tolerant, deep tolerant, and long-term inundated (Gosejohan et al., 2017). Only the edge, shallow tolerant, and long-term inundated community types were identified in Coyote Springs. Classification tree analysis (CART) was used to model the probability of occurrence for each plant community group at Coyote Springs according to habitat requirement thresholds of hydroperiod and maximum water depth at an annual resolution. Because hydrologic data were collected for a single year, whereas some of the plant species present were perennial species that persist for multiple growing seasons, it was assumed that the year of sampling was broadly representative with respect to the habitat requirements of dominant plant species.

Table 2
Calibration parameters for Coyote Springs vernal pool hydrologic model.

Parameter Name (Unit)	Definition	Calibrated Value
InitialSoilStorage (m^3)	Boundary condition	2257
α_{Soil} (unitless)	soil actual evapotranspiration coefficient (Eq. (1))	0.15
α_{Water} (unitless)	water actual evapotranspiration coefficient (Eq. (2))	1.01
a_1 (°C)	air temperature above which all precipitation is rain (Eq. (6))	3.7
a_2 (°C)	air temperature above which snow melting begins (Eq. (6))	−10.8
SeepageCoeff (unitless)	seepage loss factor (Eq. (11))	2.98
BasinSoilFactor (unitless)	factor that partitions precipitation between soil and pool when stage is increasing (Eq. (12))	0.26
SoilDepth (m)	average depth of soil between lowest pool elevation and duripan (Eq. (13))	0.334

The hydroperiod model for Coyote Springs predicted the edge community group to occur at hydroperiods of less than 101.5 days, the shallow tolerant community group to occur at hydroperiods of 101.5–209.5 days, and the long-term inundated community group to occur at greater than 209.5 days of inundation. In the maximum depth model for Coyote Springs, edge community, shallow tolerant, and long-term inundated community species were associated with maximum water depths of less than 15.5 cm, 15.5–26.87 cm, and more than 26.87 cm, respectively. Although the hard thresholds suggested by the CART model are an artifact of the statistical modeling approach and do not reflect the variability in vegetation-hydrology relationships found in nature, they provide useful information for projecting directional shifts of plant community types in response to hydrologic change. Therefore, areal coverage of each of the three plant community groups was projected according to the CART thresholds, given simulated estimates of the two hydrologic variables for various climate change scenarios.

To couple the vegetation data with stage gage data for linkage with the hydrologic model output, a total station survey of the pool was used to create a bathymetric surface from which water elevations from the stage gage could be projected to any location within the pool (see Section 3.1). Maximum depth was defined as the maximum depth of water above a given elevation within the pool. For example, if the maximum stage gauge reading for a given year was 0.24 m, the maximum depth for the portion of the pool associated with an elevation 0.00 m on the stage gauge would have a maximum depth of 0.24 m, whereas the portion of the pool associated with the elevation at 0.22 m on the stage gauge would have a maximum depth of 0.02 m. Thus, the maximum depth for each 2-cm elevation increment was calculated by taking the difference between the maximum stage gauge reading for a given year and the elevation at the location, with the deepest part of the pool having a datum value of zero. Hydroperiod was calculated by summing the number of quarter-months that the pool stage was above a given discretized 2-cm elevation. The number of quarter-months was then multiplied by 7.6 days to determine days of inundation. The model then determined which vegetation type to assign to a given area associated with each 2-cm elevation increment within the pool, according to the hierarchical classification provided by the CART analysis. The area associated within each 2-cm increment within the pool was greater than 1400 m^2 for all increments. The model output was vegetation community type as percentage of *MaxPool*.

Vernal pool specialist species are among the indicator species found in shallow tolerant and long-term inundated communities. Therefore, for the purposes of our analysis, we considered increases in long-term inundated and shallow tolerant communities as indicating increases in vernal pool specialist species habitat.

3.3. Climate data and climate change scenarios

PRISM precipitation and temperature data were used as the climate inputs for the hydrologic model for calibration and historical runs. PRISM data were used for precipitation and air temperature inputs to the model for calibration of water year 2011 by comparing model output to stage gauge data. Datasets of precipitation and minimum and maximum temperature for climate change scenarios were obtained from the bias-correction and constructed analogs (BCCA version 2), which were downscaled from the World Climate Research Programme's Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (Maurer et al., 2007; available at: http://gdo-dcp.ucllnl.org/). BCCA data are available at daily time increments and 1/8th of a degree grid size. At the time this study was developed, only CMIP3 data were available. We use all the downscaled GCMs available by the BCCA products. For a complete list of GCMs refer to Maurer et al. (2007). The B1 (emission scenario that assumes an aggressive emission reduction policy) and A2 (emission scenario that assumes unconstrained growth) scenarios were used from these models as they were respectively the most and least conservative of the commonly modeled emission scenarios from IPCC (2007). Because the GCM datasets are gridded to much larger cell sizes (~12 km) than the PRISM dataset (1 km), the PRISM dataset was used for additional bias correction. To bias correct temperature, mean temperature was calculated as the average of maximum and minimum temperature for the PRISM dataset and each GCM dataset for the period 1980–2000. The difference between the PRISM and GCM mean temperature for 1980–2000 was added to each GCM dataset. To bias correct precipitation, mean annual precipitation was calculated for the PRISM dataset and each GCM dataset for the period 1980–2000. The difference between the PRISM and GCM mean annual precipitation was calculated as a percentage difference and was used to scale the GCM precipitation values.

The hydrologic and vegetation (see Section 3.2) models were run for two ten-year time periods: 1990–1999 (historical) and 2090–2099 (future). For 1990–1999, PRISM and each bias-corrected GCM dataset was used for a total of nineteen historical model runs. For 2090–2099, the datasets for the A2 and B1 scenarios for each bias-corrected GCM were used for a total of thirty-six future model runs.

Differences were calculated between the 10-year means of the hydrologic model results for hydroperiod and maximum depth between historic (1990–1999) and future (2090–2099) time segments for each GCM and emission scenario. Results of vegetation models were compared using box plots for each GCM and averages of the GCMs.

4. Results

4.1. Hydrology

The parameter values for the hydrologic model that produced the smallest amount of error for Coyote Springs yielded an RMSE + *HydroperiodLengthDiff* of 0.025 m + 0 timesteps and an R^2 value of 0.962 (Fig. 4), indicating the model performed well in reproducing the hydrology of the vernal pool. The RMSE of 0.025 m was 8.9% of maximum depth.

Model results from runs with the 18 GCM inputs indicate that the average percentage of precipitation that was rain increased from 81.5% in the historic period to 94.3% for the A2 scenario and 89.9% for the B1 scenario (Fig. 5). Average hydroperiods for the historical time period (1991–2000), A2 scenario, and B1 scenario were 225 (range 207–252),

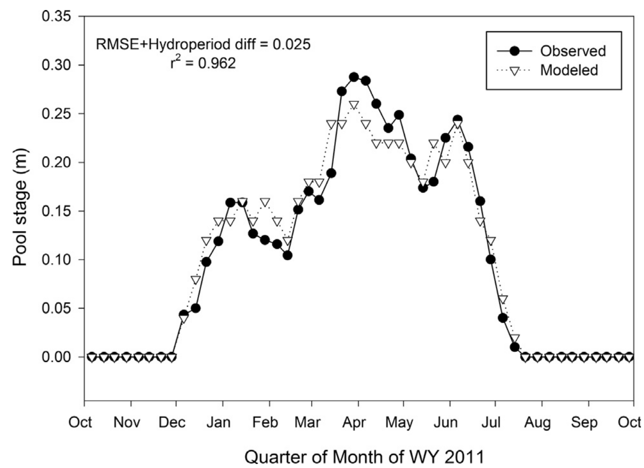

Fig. 4. Modeled and observed pool stage in Coyote Springs for WY 2011.

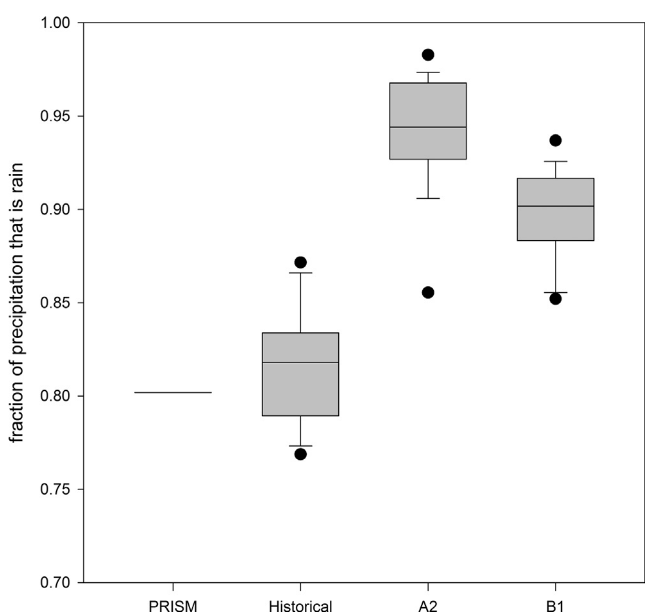

Fig. 5. Fraction of precipitation that is rain from the hydrologic model for the PRISM (1990–1999), historic GCM (1990–1999) and future GCM (2090–2099; A2 and B1 emissions) scenarios.

193 (range 144–226), and 204 (range 172–223) days, respectively (Fig. 6a). The historical period had longer hydroperiods than either of the two climate change scenarios (Fig. 6a). There was little change in maximum depth for decadal averages among all emissions scenarios (Fig. 6b); the historic mean was 26 cm (range 23–28 cm), the A2 mean was 27 cm (range 22–37 cm), and the B1 mean was 27 cm (range 23–32 cm).

4.2. Vegetation

Because the predicted change in maximum depth did not differ significantly among emission scenarios (Fig. 6b), we used only hydroperiod (and not maximum depth) to simulate changes in the vegetation community. When averaging GCM results by emission scenario, the mean historical (1990–1999) edge community type occurred in 44.5% of the pool (Fig. 7) and increased for future emission scenarios (Table 3). The model indicated a transition from the long-term inundated community to the edge and shallow tolerant communities for both climate scenarios as compared to historical conditions.

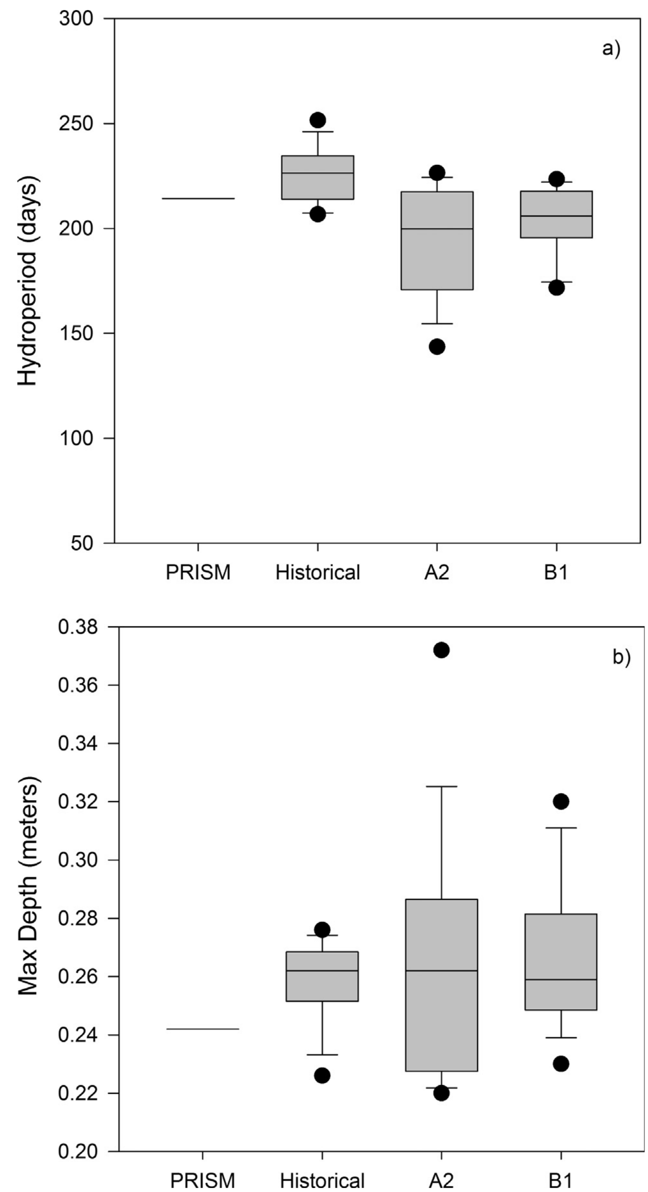

Fig. 6. Box plots of a) hydroperiod and b) maximum depth results from the hydrologic model for the PRISM (1990–1999), historic GCM (1990–1999) and future GCM (2090–2099; A2 and B1 emissions) scenarios.

5. Discussion

5.1. Susceptibility of vernal pool hydrology and vegetation to climate change scenarios

Winter (2000) noted that because many wetlands rely on precipitation as their main source of water input, they can be more susceptible to climate change. Vernal pools are seasonal wetlands and the pools studied also have little watershed inputs besides precipitation. Precipitation for the study area is projected to remain unchanged in the next century (Dettinger and Cayan, 1995) and the CMIP3 GCM data for our study area showed very similar timing and amounts of precipitation in future emission scenarios when compared to the historical time period. This resulted in little change in maximum depth values between the historical and future scenarios because similar amounts of water entered the pool primarily in the winter months when most precipitation occurs and ET is minimal. Our simulations therefore indicated more response to temperature in the summer because it affects evaporation. Air temperature was higher for both future emission

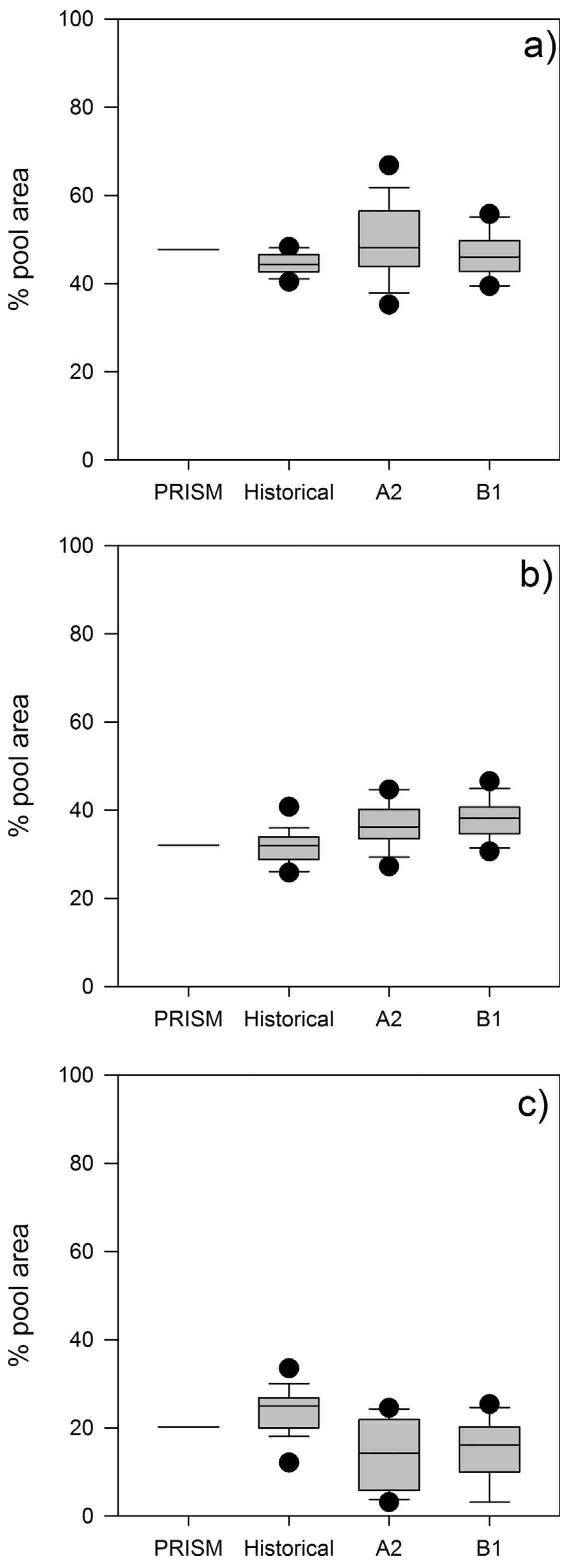

Fig. 7. Box plots showing predicted areas occupied by a) edge, b) shallow tolerant, and c) long-term inundated vegetation communities, based upon model outputs for hydroperiod.

scenarios, with A2 being more pronounced, which resulted in faster drying of the pools, shorter periods of inundation, and greater percentages of rain versus snow precipitation (Figs. 5 and 6).

The 18 GCMs in our study only had an average of 7% and 4% increase in precipitation for the A2 and B1 scenarios, respectively, as compared to historical conditions, which may have contributed to the stronger responses to air temperature in our simulations. We note that updated climate change scenarios from CMIP5 (Taylor et al., 2012) indicate that upper atmospheric large-scale dynamics can lead to an increase in northern California winter precipitation in the late 21st century (Neelin et al., 2013). Future work is necessary to understand potential impacts and uncertainty of such large-scale dynamic changes over northern California's complex terrain, as such changes could affect precipitation climate projections.

Table 3
Change in % area (Δ% area) of vegetation community as compared to results for the historical time period. Results are averages of all GCMs by time period. Positive numbers indicate an increase in % area. Total community change is determined by summing all positive change values. # indicates the number of 18 GCMs that showed a decrease in each vegetation community.

Vegetation Community	A2		B1	
	Δ % Area	#	Δ % Area	#
Edge	5.4	5	1.9	6
Long-Term Inundated	−10.2	14	−7.9	16
Shallow Tolerant	4.8	5	6.0	2
Total Community Change	10.2		7.9	

Pyke (2005) modeled climate change scenarios that increased precipitation by 10% for each 1°C increase in air temperature for Central Valley vernal pools and concluded that hydroperiod increased and consequently conditions for branchiopod reproduction improved with climate change. Precipitation in the Pyke (2005) study was increased by as much as 30%, whereas the GCMs we used had average increased precipitation for our study area of 2.1% for A2 and 2.5% for B1 scenarios per degree C increase in air temperature, which could explain the differences between that study's results and ours for hydroperiod. We argue that our approach is more robust because it uses more recent climate scenarios and downscaled GCM data rather than assuming a constant increase in temperature and precipitation. Our approach suggests that climate change scenario conditions for vernal pool specialists may become more challenging than those shown by Pyke (2005).

Our simulations suggest that both climate change projections considered would result in sharp reductions in hydroperiod, which in turn would lead to declines of the long-term inundated community, whereas edge and shallow-tolerant communities would increase. The vernal pool specialist species of primary conservation concern are more commonly found in the long-term inundated community, where extended seasonal periods of inundation act as an ecological filter to exclude both wetland generalists and invasive plant species (Javornik and Collinge, 2016; Gosejohan et al., 2017). Previous studies have also found the hydroperiod to be critically important for determining plant community structure in vernal pool ecosystems (Bauder, 2000; Deil, 2005; Emery et al., 2009; Gosejohan et al., 2017).

5.2. Hydrologic modeling approach

The objective of this study was to develop and apply a modeling approach linking climate, hydrology and vegetation dynamics for vernal pools. The simple water balance approach performed reasonably well for the Coyote Springs vernal pool in terms of modeling hydroperiod and water depth over time. Although Pyke (2004) suggested that less than daily time steps would be better for modeling vernal pool hydrologic processes in his models of Central Valley and coastal vernal pools in California, we had similar limitations in data availability to the Pyke (2004) study and found the weekly time step to be appropriate for this vernal pool in northern California given the uncertainties of the data used to model the system. We prioritized fitting the timing and duration of the hydroperiod in testing model fit because of the objective

of linking hydrology and vegetation. The Coyote Springs hydrologic model used surveyed topography to develop a relationship between pool volume and water depth that was more geometrically resolved than the representation used by Boone et al. (2006) and Pyke (2004). Thus, the model represented the more complex geometry of Coyote Springs where deeper regions of the vernal pool had steeper slopes than the edge of the pool. Unlike Boone et al. (2006) who modeled vernal pools in Minnesota, we did not explicitly include surface water inflow from runoff to the pool because of the very small watershed surrounding the pool, but we did include calculated snowmelt at each timestep.

5.2.1. Limitations of the hydrologic modeling approach

The ET method used for this study was simple and based on air temperature only. While there is some evidence that temperature-based ET methods such as Hamon (1963) are better than radiation-based estimates such as the Priestly-Taylor approach in humid environments (Lu et al., 2005), it would be preferable to use Penman-Monteith or a fully physical ET model such as that used in Donohue et al. (2010) given the dry conditions at the site. In addition, the use of a constant relationship between AET and PET in the model does not represent some dynamics associated with soil drying that could affect ET and vegetation. However, when considering the period of interest in this study is 2090–2099, there is large uncertainty associated with many of the Penman-Monteith input parameters (e.g., solar radiation that is dependent on cloud cover), as well as other input parameters that are unavailable (ground heat flux) from climate models. Furthermore, the large difference in size between climate model cells and the Coyote Springs site makes downscaling many of the parameters inappropriate. McVicar et al. (2012) found broad decreases in wind across the globe in recent decades that resulted in Penman-Monteith overestimating ET. Given the scope of the study and current climate data available, the use of a temperature-based model was most appropriate. Some models have used a water stress factor that is a function of soil depth and water content to estimate AET from PET (e.g., Arnold et al. 1998), which could be an appropriate modification of our approach to better represent the relationship between AET and PET. However, our approach did include separate calibration parameters for a soil factor and an open water factor (Eqs. (1) and (2) and Table 2), which may somewhat indirectly account for water stress. The modeling approach used in this study could also be strengthened when climate parameters such as wind speed and vapor pressure become available with more certainty in the climate modeling data set so that radiation and physically-based ET methods could be applied.

We also acknowledge that there is uncertainty in the future projections of temperature and precipitation, and hence our estimates of ET. Because of that uncertainty, we used all 18 GCMs and two emissions scenarios (i.e., A2 and B1) to examine future conditions.

Regarding snow accumulation and melt, the parameter for which snow begins melting (a_2) was calibrated to be $-10.8\,^{\circ}$C. While this temperature is considerably lower than the freezing point of water, snowmelt is a function not only of temperature, but also of short- and longwave radiation. Coyote Springs is free from large vegetation and other objects that could provide shade from solar radiation, which could lead to snowmelt occurring at temperatures below the freezing point.

The use of a constant partitioning between soil water and open water was a simplification that could be improved upon with more data. As pool stage increases, per unit of stage increase requires more water to both wet the soil and fill the pool because of the expanding pool perimeter and area. While partitioning of water between the soil and the pool in reality is a head dependent process, determination of the head dependence would require a duripan survey which was not possible for this study.

5.3. Data limitations

Model development, calibration, and validation were limited by data availability. We were only able to collect data over one year at one vernal pool (Coyote Springs), so the model was only calibrated for that particular year and location. Ideally, the model would have multiple years of data for calibration. While all processes simulated within the model would benefit from more calibration data, parameters that directly affect initial pool formation for a given year (e.g. *SoilDepth*) would in particular benefit from additional data. Initial pool formation is responsive to antecedent hydrologic factors, therefore multiple years of data would be preferable for calibrating the model.

Data were not available for an independent validation of the model. Assessment of model generalizability will require applying the model to additional vernal pools that vary in soils, morphology, climate and other variables. This in turn would benefit from long-term data collection for hydrologic variables and plant community structure, across a diverse network of monitoring sites.

5.4. Suggestions for future work

Overall, the coupling of hydrologic and vegetative models is a promising approach to quantify changes in vernal pool plant communities under a variety of climate scenarios. Previous studies have applied similar approaches to couple process-based hydrologic models with empirical models of vegetation response to hydrology, for riverine systems and wet-meadow communities (Auble et al., 1994; Springer et al., 1999; Rains et al., 2004; Hammersmark et al., 2010). In this study, we used output of water depth with a statistically-derived vegetation model to examine the potential impacts of climate change projections on vernal pool vegetation communities. We do have several suggestions for future work that could improve this approach.

We used statistics with field data to establish the relationships between vernal pool vegetation and hydrology, but more mechanistic information on this relationship would strengthen process modeling efforts. While some studies have tried to isolate the effects of hydrology on the germination process of vernal pool plants in a controlled laboratory setting (e.g., Bliss and Zedler, 1998), more laboratory experiments would be beneficial for determining hydrologic thresholds while controlling for confounding variables (e.g., isolating the effect of hydroperiod from that of seasonally varying water depths).

In addition, many factors that are species specific besides hydrology can influence plant community structure. A coupled model that considers other variables in addition to hydroperiod and maximum depth would likely improve modeled results. Possibilities for model variables include pH, water temperature, and soil texture.

We also encourage collecting more data and developing a more mechanistic modeling approach. Data collection from multiple pools over longer periods of time to allow more robust testing and calibration of hydrologic and vegetation models. Such data would also enable the development of a mechanistic hydrologic modeling approach for a more generalized process-based understanding of vernal pool hydrology. In addition, better data would enable the use of more physically-based ET approaches.

6. Conclusion

Previous studies (Bauder, 2000; Gosejohan et al., 2017, etc.) have indicated that hydrology is a central driving environmental factor for determining ecological community distribution within vernal pools. In this study, a modeling approach that combined hydrology and vegetation models was developed and used to investigate the potential implications of climate change on vernal pool hydrology and specialist species in northern California. Results indicate that climate change could lead to shorter hydroperiod which could be challenging for vernal pool specialist species. Additional studies of vernal pools with coupled

hydrology and vegetation and faunal models would enable better understanding of implications of climate change for vernal pools in wetter or warmer climate regions. Such coupled models can help resource managers to assess the relative effectiveness of alternative hydrologic restoration scenarios for mitigating climate change effects on these unique ecosystems.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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